

RESEARCH PAPER

Non-crop habitats concurrently drive crop colonization by the millet head miner and regulation by natural enemiesAhmadou Sow^{a,b,c,*}, Valérie Soti^{a,c,d}, Ibrahima Thiaw^{a,d}, Thierry Brévault^{b,c}^aCIRAD, UPR AIDA, F-34398 Montpellier, France^bCIRAD, UPR AIDA, Biopass, Centre de recherche ISRA-IRD, Dakar, Senegal^cAIDA, Univ Montpellier, CIRAD, Montpellier, France^dCSE, Fann Résidence, BP 15532 Dakar, Senegal

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Abstract

Non-crop habitats, depending on their composition, can enhance the abundance and diversity of natural enemies of crop pests, but also at the same time provide resources to pests, thereby reducing the effect on pest incidence and resulting yield losses. The objective of the present study was to test (1) the effect of semi-natural habitats in the landscape on crop colonization by pests and natural regulation, and (2) the relationship between natural regulation and pest incidence. The pearl millet head miner (MHM) was selected as a case study because it is a key pest of millet cultivated in traditional pesticide-free tree-crop agroforestry systems in which its control mostly relies on the action of natural enemies.

A set of 24 millet fields were selected in a 20×20 km area in Senegal, from the analysis of high-resolution satellite images (Pléiades), and hypotheses on the relative abundance of semi-natural habitats (here trees and rangelands) in the agricultural landscape. Millet fields were monitored for pest infestation of panicles and pest natural regulation. We used partial least squares structural equation modelling (PLS-PM) to evaluate the relationships between the abundance and diversity of semi-natural habitats at the landscape scale, crop colonization, natural pest regulation, and pest incidence.

Panicle colonization by the MHM was generally high (14–92%) and increased with the abundance of trees and to a lesser extent with the rangeland area at a 1000 m-radius around millet fields. However, regulation provided by natural enemies was amplified by the abundance of trees at a local scale (250 m-radius around millet fields). This was particularly true at early crop colonization of the MHM with parasitism and direct predation on eggs and young larvae. This multi-scale effect of semi-natural habitats on crop colonization and natural regulation could explain why no clear relationship between crop colonization and pest incidence, nor natural regulation and pest incidence, was observed. Future studies on the identification of complex species-specific interactions between trees and natural enemies should provide a better understanding of the ecological processes underlying the performance of natural regulation of MHM populations.

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Keywords: Conservation biological control; Natural regulation; Millet-based agroecosystem; Landscape composition; Pest management; Tropical semi-arid environment

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Introduction

Environmental disruptions due to climate change and increasing human pressure on natural resources dramatically threaten biodiversity and benefits provided to human societies (Cardinale et al., 2012; Pecl et al., 2017). This is particularly true in the tropical semi-arid areas where the human population has doubled over the last 30 years, with an increasing demand for food, fiber, and energy (Laurance et al., 2014). In response to stagnating crop yields in smallholder agriculture, increasing expansion of agricultural land through deforestation combined with the reduction of fallow in space and time at the expense of natural and semi-natural habitats has led to extensive simplification of agricultural landscapes within a few decades. These radical changes are negatively impacting biodiversity (Tscharntke et al., 2005) and thereby ecosystem services that directly benefit agricultural production and food security challenges such as natural pest control (Abate et al., 2000; Grab et al., 2018; Rusch et al., 2016).

Generally, natural pest control increases with landscape complexity (Bianchi et al., 2006; Haan et al., 2020). In particular, semi-natural habitats provide important life support functions to a range of natural enemies (Chaplin-Kramer et al., 2011; Kebede et al., 2018; Rusch et al., 2013; Soti et al., 2019; Veres et al., 2013). However, a recent meta-analysis by Karp et al. (2018) noted that the effect of non-crop habitats on pests and biological control by natural enemies does not show a consistent trend. Different scenarios of when and why natural habitats may fail to support the biological control of pests have been proposed by Tscharntke et al. (2016): lack of effective natural enemies, habitat as a greater source of pests than natural enemies, crops providing more resources for natural enemies than does natural habitat, availability or accessibility of resources to provide large enough natural enemy populations, or agricultural practices counteracting enemy establishment and biocontrol. The relative importance of natural habitats for biocontrol can vary dramatically depending on the type of crop, pest, natural enemies, farming systems, and landscape structure (Tamburini et al., 2020). For this reason, conservation or restoration of semi-natural vegetation to improve biological control should rely on a system-wide approach considering the life system of target crop pests and their natural enemies at the landscape scale (Brévault & Clouvel, 2019; Duarte et al., 2018; Gurr et al., 2017).

In the "Peanut basin" of Senegal (West Africa), agricultural landscapes are characterized by traditional agroforestry parklands in which trees are distributed in and around cultivated areas (Leroux et al., 2022; Soti et al., 2019). Trees have generally been conserved by farmers because they offer multiple services to rural communities such as wood, feed for cattle, soil fertilization through nitrogen fixation, and carbon sequestration (Bayala et al., 2012). In addition, Leroux et al. (2022) showed that tree abundance and tree species richness were positively associated with the grain yield of pearl millet, as an essential staple crop in these agricultural

landscapes. However, a key insect pest, the pearl millet head miner (MHM) (*Heliocheilus albipunctella* de Joannis) (Lepidoptera, Noctuidae) is a permanent threat to increasing crop yields (Gahukar & Ba, 2019; Sow et al., 2018). Moths emerge from the soil one to two months after the beginning of the rainy season. After mating, females lay eggs in the millet panicle on the silk of the flower involucre or under stamens, but also on the floral peduncles or on the spine (Nwanze & Harris, 1992). Newborn and young larvae (1–7 days old larvae) perforate glumes and consume flowers, while the older ones (8–18 days old larvae) cut off the floral peduncles (Gahukar, 1984; Vercambre, 1978), thus preventing grain formation. Outbreaks of MHM are observed almost every year, especially on early planted or early maturing millet, and yield losses up to 85% (Gahukar & Ba, 2019). In the absence of any insecticide application by farmers, millet production relies on pest regulation by natural enemies (Bhatnagar, 1987; Payne et al., 2011; Sow et al., 2019, 2020a).

A previous study conducted in the northern part of the Peanut basin (Bambey) showed that the abundance of trees, mainly acacia trees, dominated by *Faidherbia albida* (Delile) (Fabales, Fabaceae), fostered the biological control of the MHM (Soti et al., 2019). Such ecological relationships have not been investigated to date in the southern part of the Peanut basin (Nioro) where the composition and relative abundance of semi-natural habitats greatly differ from that of the northern part due to different soil and rainfall conditions. In the southern part of the Peanut basin, semi-natural vegetation is dominated by shrubs and herbaceous vegetation that form rangelands (transhumance corridors for cattle), and other tree species such as *Cordyla pinnata* (Lepr. ex A. Rich.) Milne-Redh. and *Parkia biglobosa* (Jacq.) Benth. (Fabales, Fabaceae) (Diatta et al., 1998). In addition to the previous study by Soti et al. (2019), we here addressed the effect of semi-natural vegetation on crop colonization by MHM moths and we described the parasitoid community associated to MHM eggs and larvae. We hypothesized that (i) the abundance and diversity of semi-natural habitats at the landscape scale decrease crop colonization by the pest and increase its regulation by natural enemies (processes here expressed by parasitism rates and overall biological control on early and late stages of the MHM), and that (ii) pest regulation by natural enemies contributes to the reduction of pest incidence in millet crops. Results are discussed in the light of those obtained by Soti et al. (2019) on the effect of trees on natural regulation of the MHM in a different landscape context in the Senegalese Peanut basin.

Materials and methods

Study area and design

A field survey was conducted in the southern part of the Senegal "Peanut basin" (Fig. 1A), around Nioro du Rip (13°

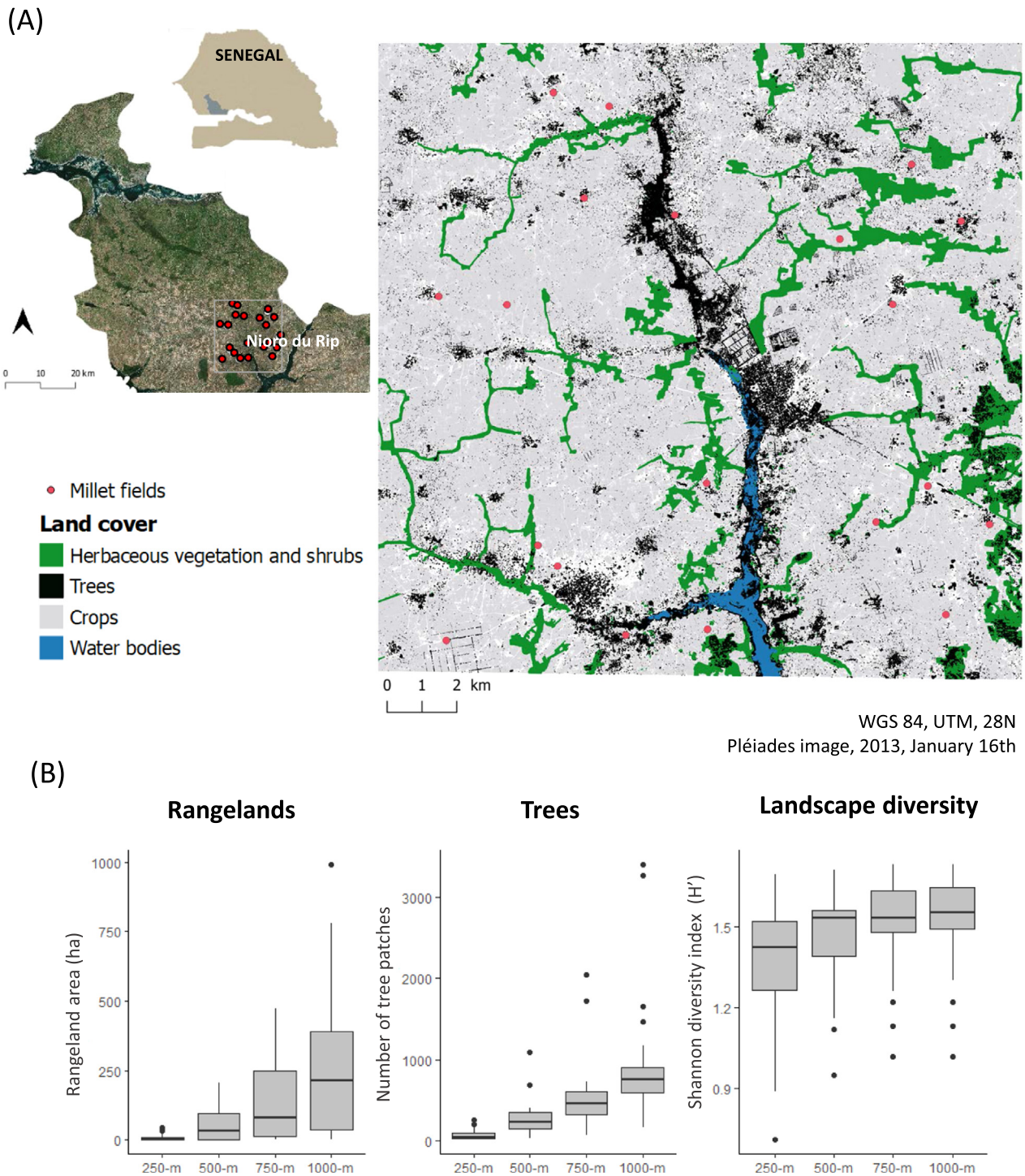


Fig. 1. (A) Map of the 24 millet sampling plots in the study area (Nioro du Rip, Senegal). Infrared colored Pléiades image from 2013, January 16th, ©CNES 2013, distribution Airbus DS/ Pléiades Image/ISIS programme. Rangelands are grazing corridors for cattle that consist of herbaceous plants and shrubs. (B) Mean, minimum, and maximum of the number of tree patches, rangeland area, and landscape diversity (SHDI) around millet fields at four spatial scales (from 250 to 1000 m-radius).

45°20.39"N; 15°47'12.29"O). This area is under the influence of a Sudano-Sahelian climate with more rain and greater soil fertility than in the northern part (700–800 vs. 400–500 mm) where the reference study (Soti et al., 2018, 2019) was conducted. The landscape is composed of field

crops (pearl millet, peanuts, cowpea, and maize) with trees mainly including *C. pinnata* and *P. biglobosa* (Diatta et al., 1998). Rangelands are composed of a diversity of bushes and shrubs (mainly Combretaceae including *Combretum* spp. and *Guiera senegalensis* J.F. Gmel., and Fabaceae

including *Piliostigma reticulatum* (D.C.) (Hochst.). A set of 24 focal millet fields were selected within an area of about 20×20 km and monitored during the 2015 and 2016 cropping seasons (Fig. 1A). Focal fields were selected along a gradient of abundance of semi-natural habitats (rangeland area and number of tree patches) in their surrounding landscape (1-km radius) (Fig. 1B). Fields were selected at least 2 km from each other to avoid spatial dependence of observation units.

Landscape metrics

A Pleiades satellite image was acquired on January 16th, 2013, with a ground resolution of 0.5 × 0.5 m in the panchromatic mode, and 2 × 2 m in the multispectral mode, with blue (B), green (G), red (R) and near-infrared (NIR) bands. In March 2013, a land-cover field survey was conducted in the study area to identify main vegetation types. The ‘multi-resolution segmentation’ algorithm in the ENVI Feature Extraction Module 5.1 was used to obtain meaningful landscape objects from the image. With a sample of 835 ground truth sites (out of the 1462 visited ones) as training data, the large image-object scale was classified into five land cover classes including rangelands, trees, crops, water bodies, built up areas, and roads. The classification accuracy was evaluated using ground truth data (732) that were not used in the classification process. The land-cover map validation showed a good match between the predicted and observed classes with a global accuracy rate of 80.7% of ground truth pixels correctly classified. Then, from the land cover map, three landscape variables were calculated at four different spatial scales (from 250 to 1000 m-radius) around the set of 24 focal millet fields, using the Fragstat software (McGarigal, Cushman, Neel, & Ene, 1995): (i) number of tree patches, (ii) area covered by rangelands, and (iii) Shannon diversity index (H') of vegetation classes including crops, trees, and rangelands (Fig. 1B).

Crop colonization and pest incidence

Crop colonization was monitored by counting the number of eggs and neonates at the early flowering stage on 50 millet panicles from 50 plants in each focal field. MHM incidence was monitored by counting the number of larvae at the grain filling stage on 50 millet panicles from 50 plants. Millet plants were randomly selected along 4–5 parallel S–N transects covering the entire field. Sampling began a short distance inside the field to avoid border effects. Egg counting, as an indicator of crop colonization by the pest, was performed by a careful inspection of both sides of panicles (from panicle emergence to female flowering) with forceps to look for eggs on floral pedicels or glumes, whereas panicles were entirely inspected for larvae counting.

Parasitism rates and diversity of parasitoids

MHM eggs and larvae were sampled in the 24 millet fields at panicle emergence and grain filling, respectively, and reared in the laboratory for diagnosis of parasitism (Sow et al., 2018). A total of 2326 eggs (23–130 per millet field) were collected in millet fields, sorted in small pillboxes (10–25 eggs per box), and incubated at room temperature up to larval hatching or emergence of parasitoids. A total of 3945 larvae (104–188 per millet field) were randomly collected from millet panicles and individually incubated at room temperature in 12-well culture plates (Fisher Scientific, France) filled with artificial diet (Southland Products, USA), up to pupation or the emergence of parasitoids (Sow et al., 2019). Parasitism rates were calculated as the ratio of the number of parasitized eggs or larvae to the number of hatched eggs or live larvae (see Sow et al., 2019). The Shannon diversity index (H') was used to assess the diversity of parasitoid species (Shannon, 1948). All parasitoid species were identified by specialists (see Acknowledgments) and by using taxonomic keys (Delvare & Aberlenc, 1989; Huddleston & Walker, 1988) or by comparing them with reference collections held at the British Museum (London, UK) or at the Centre de Biologie pour la Gestion des Populations (CBGP, Montpellier, France).

Biocontrol services index (BSI)

In each millet field, biological control of the MHM populations was evaluated by experimentally excluding natural enemies from naturally infested millet panicles, according to Soti et al. (2019). Natural enemies including arthropod predators and parasitoids, but also insectivorous birds, were excluded from panicles with mesh bags (15×70 cm) from 0 to 9 days (no access to eggs and young larvae, BSI 0–9) or from 9 to 18 days (no access to L3–L4 larvae, BSI 9–18) after panicle flowering. Open naturally-infested panicles were concurrently monitored as a control. Five replicates of each panicle type were set up in each millet field. The number of MHM larvae on each panicle was counted at 18 days after panicle flowering. A Biocontrol Services Index (BSI) adapted from Gardiner et al. (2009) was then calculated for each of the three treatments and for each millet field, by using the following formula:

$$BSI = \frac{\sum_{n=1}^n \frac{M_{0p} - T_{1p}}{M_{0p}}}{n} \times 100$$

where M_0 is the number of larvae collected on protected panicles, T_1 is the number of larvae collected on open panicles, p is the batch number, and n is the number of replicates for a given millet field. The resulting BSI varied from

0 to 100%, with values increasing as the level of biological control increases.

Statistical analyses

Statistical analyses were performed in two steps: (1) pre-selection of landscape variables at the best fitting spatial scale and (2) assessment of the direct and indirect effects of landscape features on MHM crop colonization, pest incidence, and natural regulation. All statistical analyses were conducted using the R program (version 3.6.1) software (RStudio, 2012).

Landscape variables used in pre-selection and PLS-PM models were previously tested for collinearity using the pair-wise Pearson correlation matrix and the Variance Inflation Factor (VIF) at each buffer size (Smith et al., 2009) (see Appendix A: Fig. A1 and Table A1). Only predictors with non-significant inter-correlations ($VIF \leq 2$) were selected (see Appendix A: Table A1). To preselect landscape variables, a multi-model inference approach (Burnham & Anderson, 2002) was used to examine the relative importance of landscape predictors at each spatial scale on crop colonization (eggs and first-instar larvae), pest incidence (3–4-instar larvae), and components of natural regulation (BSIs, parasitism rate, and parasitoid diversity) in millet fields. This approach consists in fitting all possible linear combinations of the predictors and ranking the models according to fit balanced by a penalty for increasing numbers of parameters (Rusch et al., 2011). For a data set with k explanatory variables, there were 2^k combinations among variables (here, 8 to 16 models resulting from 2^3 to 2^4 combinations). We used this approach for each data set at the four spatial scales. Candidate models were ranked using the second-order Akaike information criterion (AICc) which is a biased-corrected version of the AIC recommended in analyses where the sample size is small relative to the number of fitted parameters (Burnham & Anderson, 2004). To find out which spatial scale was most important, we considered all 2^k combinations for each spatial scale in the same dataset and recalculated the normalized Akaike weights on this new dataset for each model (i.e., considering the $AICc_{min}$ among the dataset including all combinations of predictors at each spatial scale) (see Appendix A: Fig. A2). The relative importance of an explanatory variable at a given spatial scale was computed as the sum of the Akaike weights across all the models in the set where this variable occurred (Burnham & Anderson, 2002). The final model was obtained by combining predictors at the most relevant spatial scale in a generalized linear model (GLM). In each final model, year was considered as a fixed effect when the effect of year was significant. Models were fitted using the appropriate distribution type and link function: binomial for proportions (logit) and Poisson for count data (log). The “MuMIn”, “nlme”, and “Mass” R packages were used.

To examine complex cause-effect relationships between landscape features, crop colonization or natural regulation, and pest incidence, we used partial least squares structural equation patch modelling (PLS-PM). This approach enables to explore and predict the functioning of complex systems including correlated variables and does not have strict requirements regarding data distribution and sample size (Puech et al., 2014; Tenenhaus et al., 2005). PLS-PM is a blend of two models: a measurement model and a structural model (Durand-Bessart et al., 2020). The measurement model defines the relationships between observed variables and latent variables inside blocks, with each block being represented by a latent variable and built with observed variables (Fig. 2A). The structural model investigates relationships between latent variables using a linear regression approach. A conceptual model (Fig. 2A) was first constructed following ecologically-based relationships. The latent variable “natural regulation” was built from “the natural regulation on eggs and newborn larvae; BSI 0–9”, “and the late instar larvae; BSI 9–18”, “egg parasitism”, and “larval parasitism”, whereas “crop colonization” and “pest incidence” were built from “egg-infested” and “larvae-infested” panicles, respectively. Analyses were conducted using the “plspm” R package (Sanchez, 2013) for model building. Before obtaining the final models, we made a set of verifications and transformations (see Appendix B: Table B1) as recommended by Sanchez (2013).

Results

Crop colonization and pest incidence

The percentage of egg-infested panicles at the early flowering stage of millet was much lower in 2015 (26.3%) than in 2016 (74.2%) ($t = -10.27$, $df = 20.6$, $P < 0.001$) (Table 1). The percentage of larvae-infested panicles at the grain-filling stage was high but variable among millet fields (50.0 – 90.0%), but comparable among surveys ($t = -1.70$, $df = 12.17$, $P = 0.11$) (Table 1).

The multi-model inference showed that the abundance of trees, but also the rangeland area in the landscape at a 1000 m-radius buffer, were the most important predictors of crop colonization (Table 2; Appendix A: Fig. A2 and Table A1). The best fit structural equation model confirmed that the percentage of egg-infested panicles significantly increased with the abundance of trees and rangeland area at a 1000 m-radius (Fig. 2B; see Appendix B: Table B2). No significant relationship between crop colonization and pest incidence was observed.

Natural regulation

Natural regulation of the MHM evaluated through the exclusion of natural enemies from naturally infested panicles

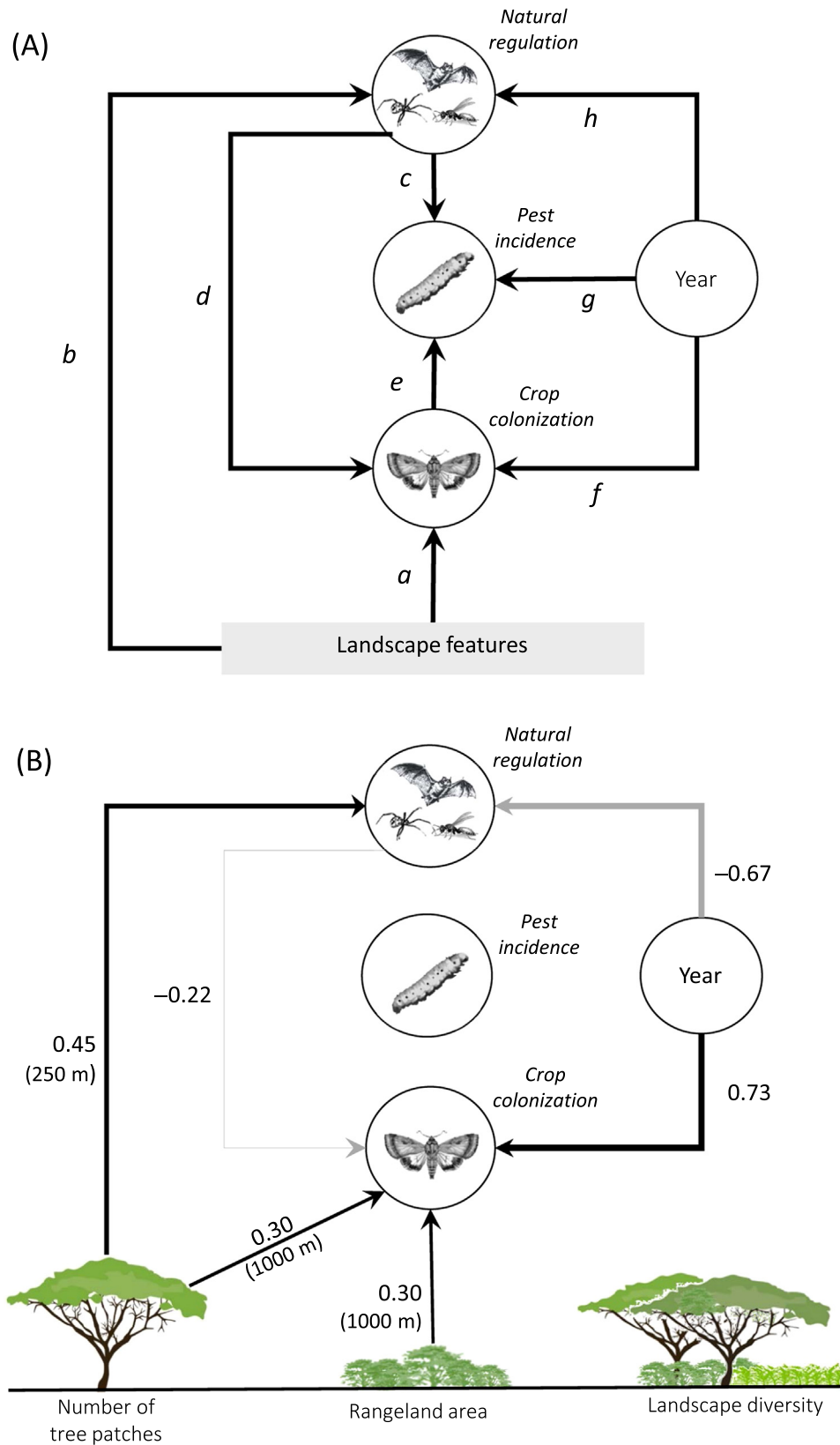


Fig. 2. (A) Conceptual model following ecologically-based hypotheses: abundance and diversity of semi-natural habitats at the landscape scale decrease crop colonization (a), increase pest regulation by natural enemies (b), thus contributing to the reduction of crop colonization and pest incidence in millet crops (c, d), and the direct effect of crop colonization to pest incidence (e). Year factor was included as explanatory variable in the model (f – h). (B) Structural equation model (SEM). Single-headed arrows represent causal relationships. Black lines

Table 1. Mean, minimum and maximum values of variables depicting crop colonization, natural regulation, and incidence of the millet head miner (MHM) in the 2015 and 2016 field surveys. BSI 0-9: Biocontrol Services Index at the early stages. BSI 9-18: Biocontrol services Index calculated at the late stages.

| Variables | | 2015 Mean (min–max) | 2016 Mean (min–max) | P |
|--------------------|---|------------------------|------------------------|----------------|
| Crop colonization | Egg-infested panicles at the early flowering stage (%) | 26.3 (14–40) | 74.2 (46–92) | < 0.001 |
| Natural regulation | BSI 0–9 (%) | 48.3 (30–60) | 42.5 (20–70) | 0.358 |
| | BSI 9–18 (%) | 73.3 (5–100) | 66.3 (20–70) | 0.470 |
| | Egg parasitism (%) | 22.6 (10–42) | 11.0 (1–27) | 0.014 |
| | Larval parasitism (%) | 47.0 (36–65) | 54.3 (22–76) | 0.243 |
| | Diversity of larval parasitoids (H') | 1.2 (0.9–1.2) | 0.9 (0.6–1.1) | < 0.01 |
| Pest incidence | Larvae-infested panicles at the grain-filling stage (%) | 70.0 (50–82) | 78.0 (60–90) | 0.114 |

Student t-tests ($P < 0.05$).

(BSI) was highly variable among millet fields (5 – 100%). The natural regulation on eggs and early-instar larvae did not differ between years, with 48.3% in 2015 and 42.5% in 2016 ($t = -0.66$, $df = 9.82$, $P = 0.52$). The natural regulation on late-instar larvae did not differ between years, with 73.3% in 2015 and 66.3% in 2016 ($t = -0.71$, $df = 11.14$, $P = 0.49$) (Table 1). Natural regulation of the MHM was lower on eggs and young larvae (BSI 0-9) than on L3 – L4 larvae (BSI 9-18) ($t = -3.75$, $df = 32.8$, $P < 0.01$) (Fig. 3A).

Egg parasitism was greater in 2015 than in 2016 ($t = 2.99$, $df = 9.73$, $P = 0.02$) and ranged from 1.0 up to 42.0% among millet fields (Table 1). Parasitoids that emerged from eggs were identified as *Trichogrammatoidea armigera*

(Manjunath, 1972). Larval parasitism was high and variable among millet fields (22.0 – 76.0%) but comparable between years ($t = -1.70$, $df = 12.17$, $P = 0.24$) (Table 1). Seven parasitoid species belonging to four families (Encyrtidae, Braconidae, Ichneumonidae, Tachinidae) and one unidentified nematode species were observed (Fig. 3B). *Copidosoma primulum* Mecet (Encyrtidae) and *Schoelandella sahelensis* Huddleston & Walker (Braconidae) were dominant with 34.3 and 51.5% of parasitized larvae, respectively (Fig. 3B). The prevalence of the four other species was relatively low (14.2%). The diversity (Shannon index H') of parasitoid species was greater in 2015 than in 2016 ($t = 4.09$, $df = 17.25$, $P < 0.01$) (Table 1).

Table 2. Relative importance of landscape variables at the most relevant spatial scale explaining crop colonization and natural pest regulation.

| Variables | Landscape variables | Est. | SE | z/t val. | RI |
|---|---------------------|-------|-------|----------|---------------|
| Crop colonization | | | | | |
| Egg-infested panicles (%) at 1000-m radius | (Intercept) | 4e+00 | 3e-01 | 11.92 | |
| | Year | 1e+00 | 8e-02 | 12.67 | 1.0** |
| | Tree abundance | 1e-04 | 4e-05 | 3.45 | 0.97** |
| | Rangeland area | 3e-07 | 1e-07 | 3.21 | 0.96** |
| Natural regulation | | | | | |
| Egg parasitism (%) at 250-m radius | (Intercept) | 2e+01 | 3e+00 | 7.7 | |
| | Year | 5e-02 | 2e-02 | 2.7 | 1.0* |
| | Tree abundance | 5e-02 | 2e-02 | 2.7 | 0.87* |
| | Rangeland area | 2e+01 | 3e+00 | 7.7 | |
| BSI 0-9 (%) at 250-m radius | (Intercept) | 3e+01 | 1e+01 | 2.1 | |
| | Tree abundance | 2e-01 | 6e-02 | 2.5 | 0.87* |
| | Rangeland area | 5e-04 | 2e-04 | 2.0 | 0.62* |

Estimate values indicate the sign of the slope. Est.: estimate; SE: standard error; z/t val.: z or t value; RI: relative importance value (sum of Akaike weights). Significant codes: .: $P = 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

represent significant positive relationships and grey lines represent significant negative relationships ($P < 0.05$). Numbers along arrows are bootstrapped standardized path coefficients. Numbers in brackets represent the size of buffers. Crop colonization and pest incidence are built from “egg-infested panicles” and “larvae-infested panicles” variables, respectively. The latent variable “natural regulation” brings together “egg” and “larval parasitism”, “BSI 0-9” and “BSI 9-18”.

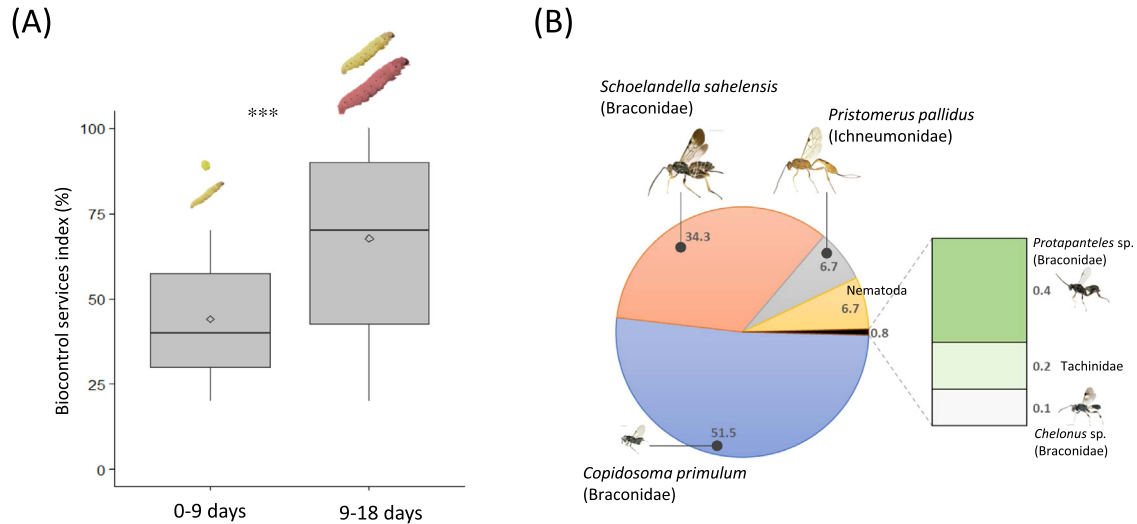


Fig. 3. (A) Boxplots of biocontrol services index (%) of eggs and early-instar larvae (0–9 days panicle post-flowering) and late-instar larvae (9–18 days panicle post-flowering), calculated from natural enemy-exclusion experiments in the 2015 and 2016 field surveys. The statistical difference between BSIs was assessed using a Student t-test. (B) Prevalence of seven parasitoid species emerged from the 3945 larvae collected from 24 millet fields.

The abundance of trees and rangeland area at a 250-m radius around millet fields were significant predictors of egg-natural regulation as evidenced by egg parasitism and BSI 0–9, but no effect of landscape composition and diversity on the percentage of larval parasitism, the diversity of parasitoids, and the BSI 9–18 was observed (Table 2; see Appendix A: Fig. A2 and Table A1). The best fit structural equation model confirmed that natural regulation on eggs and young larvae (BSI 0–9) significantly increased with the abundance of trees and rangeland area (Fig. 2B; see Appendix B: Table B2). In addition, natural regulation negatively affected crop colonization in millet fields (Fig. 2B; see Appendix B: Table B2), but no significant relationship between natural regulation and pest incidence was observed.

Discussion

Outbreaks of insect pests in agricultural systems associated with non-crop habitats are often mitigated by the positive impact of natural enemies (Rusch et al., 2010; Tschamtké et al., 2016; Veres et al., 2013). Non-crop habitats, depending on their composition, can enhance the abundance and diversity of natural enemies, but also at the same time provide resources to pests, thereby reducing the effect of natural regulation on pest incidence and resulting yield losses (Duarte et al., 2018; Santoiemma et al., 2018).

Effect of semi-natural habitats on crop colonization by the MHM

Abundance of trees and rangeland area in the agricultural landscape at a 1000 m-radius buffer around millet fields

significantly increased the proportion of egg-infested millet panicles. Trees and rangelands in the agricultural landscape probably act as refuges for moths during the day. The scale (1000 m) possibly reflects the dispersal range of moths and their ability to forage within a large area. Tree abundance (here the number of tree patches) had a greater contribution than the rangeland area to the proportion of egg-infested panicles. It is possible that tree trunks are better refuges than shrubs for moths, with the ability to avoid light and predators when hidden in cavities or under bark and more suitable microclimate. The significant difference in egg-infested panicles between 2015 and 2016 was probably due to an earlier passage during egg counting on millet panicles in 2015 and a staggering of heading that allowed egg-laying afterward, as no difference between years was observed for larvae-infested panicles at the grain-filling stage.

Effect of semi-natural habitats on natural regulation

In a previous study in the northern part of the Peanut basin in Senegal, Soti et al. (2019) showed that natural pest regulation increased with the abundance of trees and vegetation diversity (including crops) in a 1750 m-buffer around millet fields. Here, we also showed that the abundance of trees in the agricultural landscape significantly increased regulation of the MHM (evidenced on egg parasitism and BSI 0–9 days), but at a local scale of 250 m-radius around millet fields. This is probably due to the life system of natural enemies, particularly egg parasitoids and generalist predators, whose broad host range can limit their area of action. Generalists would tend to exploit available resources in at a lower spatial scale than specialists do (Symondson et al., 2002).

Here, the only observed egg parasitoid, *T. armigera*, has probably a low dispersal ability as shown for other Trichogramma species (Gardner et al., 2012; Karimoune et al., 2018). In the present study, habitat fragmentation resulting from the lower density of trees in the southern part of the Peanut basin compared to the northern one (Soti et al., 2019) could also explain the local effect of natural regulation. The positive effect of trees on egg parasitism was not true for larval parasitism. This might be explained by a wider dispersal ability of the main parasitoids, *Copidosoma primulum* Mecet. and *Schoelandella sahelensis* Huddleston & Walker, contributing to 86% of larval parasitism. In addition, these two specialist species have a life cycle synchronized with that of the MHM, with diapause throughout the dry season. It is thus possible that they do not depend on alternative resources provided by semi-natural habitats.

Effect of natural regulation on pest incidence

Natural regulation was variable between millet fields and year (egg parasitism), but comparable to that observed in the Bambey area (Soti et al., 2019). The low rate of egg parasitism (16.8%) compared to the BSI calculated on eggs and young larvae (45.4%), suggests a major contribution of arthropod predators of early stages of the MHM. Natural regulation was greater for late-instar larvae (BSI 9–18) than for eggs and young larvae (BSI 0–9), possibly due to the important contribution of the two specialist parasitoids *C. primulum* and *S. sahelensis* (Sow et al., 2019), but also vertebrates such as birds (Sow et al., 2020a). The present study did not assess the effect of moth predation by generalist vertebrate predators such as birds and bats on crop colonization by the MHM as done by Sow et al. (2020b).

Conclusions

In the present study, early panicle infestation by the MHM increased with the abundance of trees and to a lesser extent the rangeland area at a 1000 m-radius around millet fields. However, natural regulation provided by natural enemies was also amplified by the abundance of trees, but at a local scale (250 m-radius around millet fields). This was particularly true for the natural regulation of early (vs. late) stages of the MHM. This multi-scale effect of semi-natural habitats on crop colonization and natural regulation could explain why no clear relationship between crop colonization and pest incidence, nor natural regulation and pest incidence, was observed. From an applied perspective, the present study shows that conserving trees in the form of tree-crop agroforestry systems should enhance ecosystem services such as natural pest regulation, thereby reducing millet yield losses due to the MHM. However, further research efforts on species-specific interactions between semi-natural vegetation and natural enemies are needed to provide a

better understanding of the ecological processes underlying the natural regulation of MHM populations, with the aim to identify beneficial tree species. Overall, our study supports a better consideration of the value of maintaining and restoring semi-natural habitats in the agricultural landscapes of semi-arid areas of West Africa to cope with climate change and food security challenges.

Authors' contributions

Conceptualization, A.S., T.B., and V.S. - Data curation, A. S. - Formal analysis, A.S., and I.T. - Funding acquisition, T. B., and V.S. - Investigation, A.S., T.B., V.S., and I.T. - Methodology, A.S., T.B., and V.S. - Project administration, T.B., and V.S. - Resources, A.S., T.B., and V.S. - Software, A.S., I.T., and V.S. - Supervision, T.B., and V.S. - Validation, T.B. - Visualization, A.S. - Writing—original draft, A. S. - Writing—review & editing, A.S., T.B., and V.S. All authors have read and agreed to the published version of the manuscript.

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Declaration of Competing Interest

The authors declare no conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at [doi:10.1016/j.baae.2022.07.001](https://doi.org/10.1016/j.baae.2022.07.001).

References

- Abate, T., van Huis, A., & Ampofo, J. K. O. (2000). Pest management strategies in traditional agriculture : An African perspective. *Annual Review of Entomology*, 45,(1) 631659. doi:10.1146/annurev.ento.45.1.631.
- Bayala, J., Sileshi, G. W., Coe, R., Kalinganire, A., Tchoundjeu, Z., Sinclair, F., & Garrity, D. (2012). Cereal yield response to conservation agriculture practices in drylands of West Africa : A quantitative synthesis. *Journal of Arid Environments*, 78, 1325. doi:10.1016/j.jaridenv.2011.10.011.
- Bhatnagar, V. S. (1987). Conservation and encouragement of natural enemies of insect pests in dryland subsistence farming : Problems, progress and prospects in the Sahelian zone. *International Journal of Tropical Insect Science*, 8,(4) 791795. doi:10.1017/S1742758400022931.
- Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes : A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, 273, (1595) 17151727. doi:10.1098/rspb.2006.3530 Royal Society.
- Brévault, T., & Clouvel, P. (2019). Pest management : Reconciling farming practices and natural regulations. *Crop Protection*: 115 (p. 16). Elsevier Ltd. doi:10.1016/j.cropro.2018.09.003.
- Burnham, K., & Anderson, D. (2002). Model selection and multi-model inference : A practical information-theoretic approach. *Bayesian data analysis in ecology using linear models with R, BUGS, and STAN* (2nd edn). (pp. XXVI–488). Berlin: Springer.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference. *Sociological Methods & Research*, 33,(2) 261304. doi:10.1177/0049124104268644.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 5967. doi:10.1038/nature11148.
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, 14, (9) 922932. doi:10.1111/j.1461-0248.2011.01642.x.
- Delvare, G., & Aberlenc, H.-P. (1989). Les insectes d'Afrique et d'Amérique tropicale : Clés pour la reconnaissance des familles. Editions Quae.
- Diatra, M., Grouzis, M., & Faye, E. (1998). Typologie de la végétation ligneuse en zone soudanienne. *Bois et forêts des Tropiques*, 257(257), 23–36. doi:10.19182/bft1998.257.a19946.
- Duarte, G. T., Santos, P. M., Cornelissen, T. G., Ribeiro, M. C., & Paglia, A. P. (2018). The effects of landscape patterns on ecosystem services : Meta-analyses of landscape services. *Landscape Ecology*, 33,(8) 12471257. doi:10.1007/s10980-018-0673-5.
- Durand-Bessart, C., Tixier, P., Quinteros, A., Andreotti, F., Rapidel, B., Tauvel, C., & Allinne, C. (2020). Analysis of interactions amongst shade trees, coffee foliar diseases and coffee yield in multistrata agroforestry systems. *Crop Protection*, 133, 105137. doi:10.1016/J.CROPRO.2020.105137.
- Gahukar, R. T. (1984). Insect pests of pearl millet in West Africa : A review. *Tropical Pest Management*, 30,(2) 142147. doi:10.1080/09670878409370867.
- Gahukar, R. T., & Ba, M. N. (2019). An updated review of research on *Heliocheilus albipunctella* (Lepidoptera : Noctuidae), in Sahelian West Africa. *Journal of Integrated Pest Management*, 10(3), 19. doi:10.1093/jipm/pmz003.
- Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O'Neal, M., Chacon, J. M., Wayo, M. T., Schmidt, N. P., Mueller, E. E., & Heimpel, G. E. (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications*, 19,(1) 143154. doi:10.1890/07-1265.1.
- Gardner, J., Wright, M. G., Kuhar, T. P., Pitcher, S. A., & Hoffmann, M. P. (2012). Dispersal of *Trichogramma ostrinae* in field corn. *Biocontrol Science and Technology*, 22,(10) 12211233. doi:10.1080/09583157.2012.723676.
- Grab, H., Danforth, B., Poveda, K., & Loeb, G. (2018). Landscape simplification reduces classical biological control and crop yield. *Ecological Applications*, 28,(2) 348355. doi:10.1002/eap.1651.
- Gurr, G. M., Wratten, S. D., Landis, D. A., & You, M. (2017). Habitat management to suppress pest populations : Progress and prospects. *Annual Review of Entomology*, 62, 91109. doi:10.1146/annurev-ento-031616-035050.
- Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting landscape configuration effects on agricultural pest suppression. *Trends in Ecology & Evolution*, 35,(2) 175186. doi:10.1016/j.tree.2019.10.003.
- Huddleston, T., & Walker, A. K. (1988). *Cardiochiles* (Hymenoptera : Braconidae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. 78(3), 435461. <https://doi.org/10.1017/S0007485300013201>
- Karimoune, L., Niango Ba, M., Baoua, I. B., & Muniappan, R. (2018). The parasitoid *Trichogrammatodea armigera* Nagaraja (Hymenoptera : Trichogrammatidae) is a potential candidate for biological control of the millet head miner *Heliocheilus albipunctella* (de Joannis) (Lepidoptera : Noctuidae) in the Sahel. *Biological Control*, 127, 916. doi:10.1016/j.biocontrol.2018.08.003.
- Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratten, S. D., Zhang, W., ... Zou, Y. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences of the United States of America*, 115(33), e7863–e7870. doi:10.1073/pnas.1800042115.
- Kebede, Y., Bianchi, F., Baudron, F., Abraham, K., de Valença, A., & Tittone, P. (2018). Implications of changes in land cover and landscape structure for the biocontrol potential of stemborers in Ethiopia. *Biological Control*, 122, 110. doi:10.1016/j.biocontrol.2018.03.012.

- Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution*, 29,(2) 107116. doi:10.1016/j.tree.2013.12.001.
- Leroux, L., Faye, N. F., Jahel, C., Falconnier, G. N., Diouf, A. A., Ndao, B., Tiaw, I., Senghor, Y., Kanfany, G., Balde, A., Dieye, M., Sirdey, N., Alobo Loison, S., Corbeels, M., Baudron, F., & Bouquet, E. (2022). Exploring the agricultural landscape diversity-food security nexus : An analysis in two contrasted parklands of Central Senegal. *Agricultural Systems*, 196, 103312. doi:10.1016/j.agsy.2021.103312.
- McGarigal, K., Cushman, S. A., Neel, M. C., & Ene, E. (1995). FRAGSTATS: Spatial pattern analysis program for categorical maps. *Analysis*, 151, 1–122. doi:10.2737/PNW-GTR-351.
- Nwanze, K. F., & Harris, K. M. (1992). Insect pest of pearl millet in West Africa. *Review of African entomology*, 80(12), 1132–1155.
- Payne, W., Tapsoba, H., Baoua, I. B., Malick, B. N., N'Diaye, M., & Dabire-Binso, C. (2011). On-farm biological control of the pearl millet head miner : Realization of 35 years of unsteady progress in Mali, Burkina Faso and Niger. *International Journal of Agricultural Sustainability*, 9,(1) 186193. doi:10.3763/ijas.2010.0560.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change : Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214. doi:10.1126/science.aai9214.
- Puech, C., Poggi, S., Baudry, J., & Aviron, S. (2014). Do farming practices affect natural enemies at the landscape scale? *Landscape Ecology*, 30,(1) 125140. doi:10.1007/S10980-014-0103-2.
- RStudio Team. (2012). *RStudio: Integrated Development for R v.3.6.1*. RStudio, Inc.. <http://www.rstudio.com/>.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., Thies, C., Tschamtké, T., Weisser, W. W., Winqvist, C., Woltz, M., & Bommarco, R. (2016). Agricultural landscape simplification reduces natural pest control : A quantitative synthesis. *Agriculture, Ecosystems and Environment*, 221, 198204. doi:10.1016/j.agee.2016.01.039.
- Rusch, A., Valantin-Morison, M., Sarthou, J. P., & Roger-Estrade, J. (2010). Biological control of insect pests in agroecosystems : Effects of crop management, farming systems, and seminatural habitats at the landscape scale : A review. *Advances in Agronomy*, 109, 219259. doi:10.1016/B978-0-12-385040-9.00006-2.
- Rusch, A., Valantin-Morison, M., Sarthou, J. P., & Roger-Estrade, J. (2011). Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecology*, 26,(4) 473486. doi:10.1007/s10980-011-9573-7.
- Rusch, A., Valantin-Morison, M., Sarthou, J. P., & Roger-Estrade, J. (2013). Effect of crop management and landscape context on insect pest populations and crop damage. *Agriculture, Ecosystems and Environment*, 166, 118125. doi:10.1016/j.agee.2011.05.004.
- Sanchez, G. (2013). *PLS path modeling with R* (Trowchez Editions). (p. 222). Berkely: Gaston Sanchez.
- Santoemma, G., Mori, N., Tonina, L., & Marini, L. (2018). Semi-natural habitats boost *Drosophila suzukii* populations and crop damage in sweet cherry. *Agriculture, Ecosystems and Environment*, 257, 152158. doi:10.1016/j.agee.2018.02.013.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27,(3) 379423. doi:10.1002/j.1538-7305.1948.tb01338.x.
- Smith, A. C., Koper, N., Francis, C. M., & Fahrig, L. (2009). Confronting collinearity : Comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*, 24(10), 1271. doi:10.1007/s10980-009-9383-3.
- Soti, V., Lelong, C., Goebel, F., & Brévault, T. (2018). Designing a field sampling plan for landscape-pest ecological studies using VHR optical imagery. *International Journal of Applied Earth Observation and Geoinformation*. doi:10.1016/j.jag.2018.05.016.
- Soti, V., Thiaw, I., Debaly, Z. M., Sow, A., Diaw, M., Fofana, S., Diakhate, M., Thiaw, C., & Brévault, T. (2019). Effect of landscape diversity and crop management on the control of the millet head miner, *Heliocheilus albipunctella* (Lepidoptera : Noctuidae) by natural enemies. *Biological Control*, 129, 115122. doi:10.1016/j.biocontrol.2018.10.006.
- Sow, A., Brévault, T., Benoit, L., Chapuis, M.-P., Galan, M., Coeur D'acier, A., Delvare, G., Sembène, M., & Haran, J. (2019). Deciphering host-parasitoid interactions and parasitism rates of crop pests using DNA metabarcoding. *Scientific Reports*, 9(1), 112. doi:10.1038/s41598-019-40243-z.
- Sow, A., Brévault, T., Delvare, G., Haran, J., Benoit, L., Cúur d'Acier, A., Galan, M., Thiaw, C., Soti, V., & Sembène, M. (2018). DNA sequencing to help identify crop pests and their natural enemies in agro-ecosystems : The case of the millet head miner *Heliocheilus albipunctella* (Lepidoptera : Noctuidae) in sub-Saharan Africa. *Biological Control*. doi:10.1016/j.biocontrol.2018.03.007.
- Sow, A., Seye, D., Faye, E., Benoit, L., Galan, M., Haran, J., & Brévault, T. (2020). Birds and bats contribute to natural regulation of the millet head miner in tree-crop agroforestry systems. *Crop Protection*, 132, 105127. doi:10.1016/j.cropro.2020.105127.
- Sow, A., Haran, J., Benoit, L., Galan, M., & Brévault, T. (2020). DNA Metabarcoding as a Tool for Disentangling Food Webs in Agroecosystems. *Insects*, 11(5), 294. doi:10.3390/insects11050294.
- Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, 47, 561594. doi:10.1146/annurev.ento.47.091201.145240.
- Tamburini, G., Santoemma, G., O'Rourke, M., Bommarco, R., Chaplin-Kramer, R., Dainese, M., Karp, D. S., Kim, T. N., Martin, E. A., Petersen, M., & Marini, L. (2020). Species traits elucidate crop pest response to landscape composition : A global analysis. *Proceedings of the Royal Society B: Biological Sciences*, 287,(1937) 20202116. doi:10.1098/rspb.2020.2116.
- Tenenhaus, M., Vinzi, V. E., Chatelin, Y. M., & Lauro, C. (2005). PLS path modeling. *Computational Statistics & Data Analysis*, 48,(1) 159205. doi:10.1016/J.CSDA.2004.03.005.
- Tschamtké, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E. A., Martínez-Salinas, A., Meehan, T. D., O'Rourke, M., Poveda, K., Rosenheim, J. A., Rusch, A., Schellhorn, N., Wanger, T. C., ... Zhang, W. (2016). When

- natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*: 204Elsevier Ltd 449458. doi:[10.1016/j.biocon.2016.10.001](https://doi.org/10.1016/j.biocon.2016.10.001).
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8, 857874. doi:[10.1111/j.1461-0248.2005.00782.x](https://doi.org/10.1111/j.1461-0248.2005.00782.x).
- Vercambre, B. (1978). *Raghuva* spp. et *Masalia* sp., chenilles des chandelles du mil en zone sahélienne. *L' Agronomie Tropicale* (1975), 33(1), 62–79.
- Veres, A., Petit, S., Conord, C., & Lavigne, C. (2013). Does landscape composition affect pest abundance and their control by natural enemies ? A review. *Agriculture, Ecosystems & Environment*, 166, 110–117. doi:[10.1016/j.agee.2011.05.027](https://doi.org/10.1016/j.agee.2011.05.027).

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